Water relations and photosynthetic characteristics of selected trees and shrubs of riparian and hillslope habitats in the south-western Cape Province, South Africa

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Forests in the Fynbos biome of South Africa are mainly confined to riparian zones and sheltered ravines. A simple explanation for this restriction could be that the riparian trees are unable to survive the soil moisture deficits associated with the summer drought that is a feature of the mediterranean-type climate. A study was made of the water relations and photosynthetic characteristics of selected riparian trees (*Brabejum stellatifolium, Brachylaena neriifolia* and *Cunonia capensis*), and shrubs of the relatively xeric hillslopes adjoining such riparian habitats (*Protea nitida* and *P. repens*). Field measurements of xylem pressure potential, leaf conductance and net leaf photosynthesis were made in the wet winter of 1986 and during the spring and summer of 1986/7. Characteristics of microclimate and soil moisture, and leaf and canopy morphology were used to explain the observed stomatal behaviour. Despite marked differences in some leaf and canopy characteristics between hillslope and riparian species, stomatal behaviour, net photosynthesis and water-use efficiencies were very similar. Soil water potentials at 900 mm depth at the riparian site remained above –0.1 MPa throughout the study and only dropped below –0.05 MPa during the dry period. Potentials at the hillslope site frequently dropped below –0.1 MPa. The differences in soil moisture potentials at the two sites were reflected in the pre-dawn and midday plant xylem potentials but the magnitude of differences was much less than had been expected. Similarly, diurnal courses of leaf conductance and net leaf photosynthesis were very similar for hillslope and riparian species. We suggest the following reasons for the very similar patterns of physiological response: (a) soil moisture deficits at 900 mm depth at the hillslope site were rapidly recharged following relatively light rainfall events and the periods between significant rainfall events were too short to induce drought; (b) the deep-rooted hillslope shrubs behave as phreatophytes and utilize water at depth; and (c) the hillslope communities have sparse canopies and evapotranspiration was too low to dry the soils to depth. Hillslope shrubs have low capacities for resource capture and use, and it appears that their sparse canopies have not equilibrated with available soil moisture as is the case with structurally similar sclerophyllous shrubs in other mediterranean-climate regions.

Die woude in die Fynbosbioom van Suid-Afrika is veral beperk tot die oewerstreke en die beskutte bergklowe. 'n Eenvoudige verklaring vir hierdie beperkte voorkoms is moontlik dat die oewerbome die grondvogtekorte wat verband hou met die droë somer ('n kenmerk van die mediterreense klimaat) nie kan oorleef nie. 'n Studie is gemaak van die vogverhoudinge en fotosintetiese kenmerke van sekere oewerbome (*Brabejum stellatifolium, Brachylaena neriifolia* en *Cunonia capensis*) en struike van die betreklik xeriese hange wat aan sulke oewergroeiplekke grens (*Protea nitida* en *P. repens*). Veldopnames van die xileemdrukpotensiaal, blaarkonduktansie en netto blaarfotosintese is gedurende die nat winter van 1986 en die lente en somer van 1986/7 gemaak. Kenmerke van die mikroklimaat en grondvog asook van die blaar- en kroondakmorfologie is gebruik om die waargenome werking van die stomata te verklaar. Hoewel die blaar- en kroondakkenmerke van die spesies wat teen die hange groei in sommige opsigte opmerklik verskil het van dié van die oewerspesies, was die werking van die stomata, die netto fotosintese en die doeltreffendheid van watergebruik baie eenders. By die oewerligging het die grondvogpotensiaal by 900 mm gedurende die studietydperk bokant –0.1 MPa gebly en het dit slegs gedurende die droë tydperk na onder –0.05 MPa gedaal. By die hangligging het die potensiaal dikwels na onder –0.1 MPa gedaal. Die verskille tussen die grondvogpotensiaal by die twee liggings word weerspieël in die voordagbreek- en middag-plantxileempotensiaal, maar hierdie verskille was baie kleiner as wat verwag is. Die daaglikse verloop van blaarkonduktansie en die netto fotosintese was eweneens baie eenders by die spesies wat teen die hange groei en die owerspesies. Die volgende redes kan aangevoer word vir hierdie soortgelyke patroon van fisiologiese reaksie: (a) by die hangligging is grondvogtekorte by 900 mm vinnig aangevul na die voorkoms van betreklik ligte reënbuie, en die tydperk tussen betekenisvolle reënbuie was te kort om tot droogte te lei; (b) die diepgewortelde struike wat teen die hange groei het soos freatofiete gereageer en het water diep onder die grond benut; en (c) die plantgemeenskappe wat teen die hange groei het 'n yl kroondak gehad en die dampverlies was te gering om die dieper grond uit te droog. Die struike wat teen die hange groei het slegs 'n geringe vermoë gehad om omgewingsbronne op te vang en te benut, en dit blyk dat die yl kroondak van hierdie plantgemeenskap nie in ewewig was met die beskikbare grondvog nie, soos wel die geval is met struktureel-soortegelyke sklerofille struike in ander mediterreense klimaatstreke.

Keywords: Fynbos, photosynthesis, soil moisture, water relations, western Cape

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Introduction

Evergreen forests in the fynbos biome (Rutherford & Westfall 1986) of the Cape Province, South Africa, are confined largely to riparian habitats and sheltered ravines. The forests are taken to be constituted by mesophytic species and burn infrequently. The confinement of forests to sheltered habitats has been ascribed to the fact that the fynbos shrublands of the open slopes, generally taken to be more xerophytic, are often disturbed, especially by fire (Moll *et al.* 1980). However, there are several instances where fire has been excluded from fynbos adjoining forest, without there having been an immigration of forest species (Kruger 1984). This suggests that physical environmental variables rather than disturbance exclude the trees. A frequently cited hypothesis is that mineral nutrients in the soil govern the forest–fynbos boundary. Van Daalen (1980, 1984), however, found little difference in the nutrient status of forest and fynbos soils in adjacent habitats, except that significantly more potassium was available in the forest soils.

A simpler physical explanation for the confinement of forests to sheltered habitats could lie in the differences in water stress experienced by plants in the respective habitats. Hypothetically, the summer-dry mediterranean climate would be associated with seasonal soil-moisture deficits in the well-drained soils of the slopes, but there would be no deficits in the riparian habitats. Sclerophyllous plants of mediterranean-climate regions have canopy characteristics favouring conservative water use such as low leaf area indices, steeply inclined, usually narrow leaves and leaf surfaces with low absorptances to solar radiation (Tenhunen *et al.* 1987). The stomata of sclerophylls open even when plant water deficits are high. Transpiration and photosynthesis can occur even with plant xylem pressure potentials of –3.0 MPa and less (Poole *et al.* 1981).

Diurnal and seasonal variations in plant water potentials and stomatal behaviour of mediterranean sclerophylls follow characteristic patterns. Stomata characteristically tend to close around midday if ambient and hence leaf temperatures are relatively high (exceeding 25–30°C) and water vapour pressure deficits (*VPD*) exceed about 3.0 kPa (e.g. Tenhunen *et al.* 1982, 1985). This occurs at high and moderate xylem pressure potentials, but not under extreme stress. With the onset of summer drought both xylem pressure potentials and maximum leaf conductances decline (Tenhunen *et al.* 1987: 323). With this trend, maximum leaf conductances tend to be reached earlier in the morning and later in the afternoon, following the diurnal variation in water vapour pressure deficit. Under severe drought conditions leaf conductances remain low throughout the day with little fluctuation. Net photosynthesis rates tend to follow diurnal fluctuations in leaf conductance (e.g. Tenhunen *et al.* 1985), and under severe drought conditions, photosynthesis may occur primarily in the morning (e.g. Mooney *et al.* 1975).

Riparian trees and shrubs on the other hand, not being subject to seasonal moisture deficits, should be distinctly different in regard to canopy characteristics and physiological response to water stress. Diurnal and seasonal variations in water potential should be smaller than for hillslope shrubs. Stomatal response to ambient vapour pressure deficit should be weak and transpiration rates should increase as evaporative demand increases since water is freely available to the plant.

The aim of this study was to determine whether the functional characteristics of the evergreen plants in the two habitats reflected the selective influence of contrasting soil-moisture regimes. We postulated that riparian sclerophylls would not be subject to soil-moisture deficits during summer and would thus maintain higher (less negative) xylem pressure potentials than hillslope species. If riparian plants have weak stomatal control of transpiration, then we should observe marked differences in the instantaneous water-use efficiencies between hillslope and riparian species. Water-use efficiencies should be lower in the riparian trees because selection would not have favoured water conservation features. We compared leaf and canopy characteristics, water relations and photosynthetic characteristics of sclerophyllous trees and shrubs of such contrasting habitats within the fynbos landscape at Swartboskloof in the south-western Cape Province. The objective was to determine whether the predicted differences in stomatal behaviour could be observed in the field, and to describe the species concerned in terms of their morphology, anatomy, and physiology.

Study site and species

Swartboskloof (34°00′S; 18°57′E) is a transverse valley within the larger Jonkershoek valley near Stellenbosch in the Cape Province of South Africa. The site receives about 1 500 mm of rainfall annually, 67% of which falls between May and September. The summer (December to February) is relatively hot (mean maximum and minimum daily temperatures for February, the hottest month, are 27.3 and 14.5°C) and dry (8% of the annual rainfall). Winters (June to August) are cool (mean maximum and minimum daily temperatures for July, the coldest month, are 16.8 and 6.2°C) and wet (44% of the annual rainfall).

Rainfall data are from the Swartboskloof weather station (altitude 305 m), for the period 1936 to 1974, and daily mean temperatures were calculated from records for the period 1976 to 1986 (unpublished data, Forestry Branch). The longest rain-free period on record (since 1936) is 61 days. Climatic conditions during the study are shown in Figure 1.

Species were selected to represent dominant and typical trees of the riparian habitat and the two dominant shrub species in the hillslope habitat at Swartboskloof. The riparian site was on the banks of a perennial stream. The three dominant trees are *Brabejum stellatifolium* L. (Proteaceae), *Brachylaena neriifolia* (L.) R.Br. (Asteraceae) and *Cunonia capensis* L. (Cunoniaceae). The trees were rooted in the stream bank, which consists of river cobbles overlain by dark humic soil 0.2–1.0 m deep. The hillslope site was located 50 m from the stream and 30 m

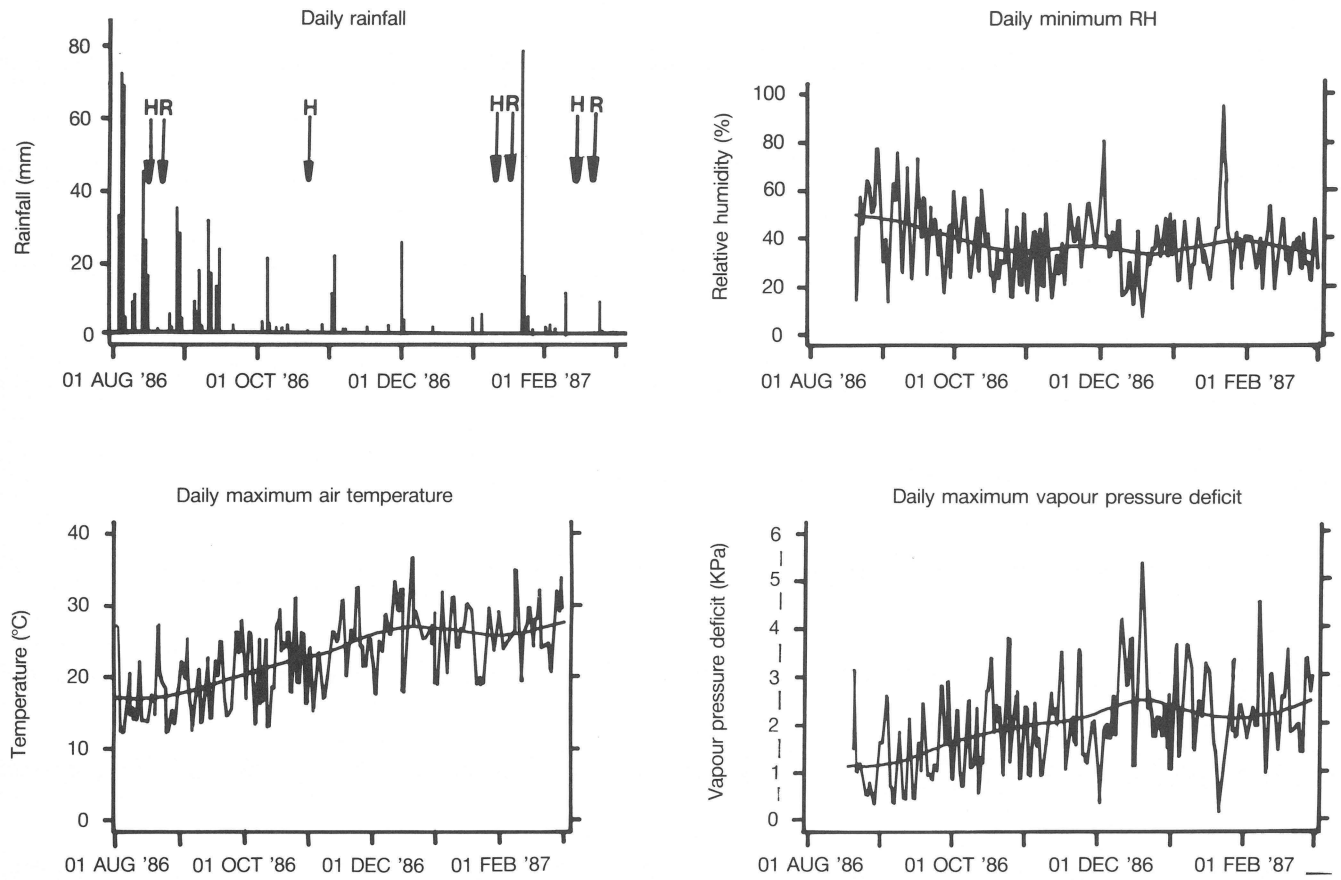

Figure 1 Daily rainfall, daily maximum temperature, daily minimum relative humidity and daily maximum vapour pressure deficit at Swartboskloof between August 1986 and March 1987. The smoothed lines, fitted by spline interpolation (SAS Institute Inc. 1985), indicate average time trends. Days on which measurements were made of plant-water relations are indicated by arrowheads (H and R indicate that measurements were made at the hillslope and riparian sites respectively).

higher, on an incline of about 30° with an azimuth of 315°. The hillslope vegetation had a post-fire age of 28 years and the two dominant shrub species at the site were *Protea repens* (L.) L. and *P. nitida* Miller (Proteaceae). The soil was a rocky sandy loam, about 0.9 m deep and freely drained.

Methods

Measurement of ambient conditions

Daily rainfall during the study was monitored at a weather station situated less than 1 km from the study site at an altitude of 305 m. Diurnal courses of relative humidity and air temperature were monitored using an automatic weather station situated approximately 500 m from the study site. Mean hourly values were calculated from readings made every minute. Daily minimum relative humidities and maximum air temperatures were used to calculate daily maximum vapour pressure deficits (the difference between saturated vapour pressure and the actual vapour pressure at the mean maximum daily temperature and mean minimum daily relative humidity).

Soil water potential

Soil water potentials were monitored at depths of 300 mm, 450 mm and 900 mm at both sites using porous-cup tensiometers with 0.1 MPa maxima. Two tensiometers were used at each depth at both sites. Spot measurements were taken at midday every 3–4 days. We were unable to measure water potentials below –0.1 MPa due to the malfunction of soil psychrometers.

Plant form and characteristics of foliage and canopy

Canopy characteristics of each species were expressed in terms of leaf dimensions, orientation, stomatal density and distribution, absorptance, leaf area index and nitrogen content. Leaf dimensions were measured on a sample of 20–30 fully expanded leaves of the current crop taken at random from a typical plant. Average orientation of the leaves was determined by measuring the angle from vertical and the azimuth of a random sample of 20 leaves on fully exposed shoots of a typical individual of each species. We calculated 'true azimuths' (Conrad & Pollak 1962: 181) from these data as a measure of average leaf orientation. Stomatal densities on ad- and abaxial surfaces were determined from electron micrographs ($n = 5$). We measured absorptance as the reciprocal of reflectance (absorptance = 1 – reflectance), the latter determined by measuring the proportion of light reflected from freshly harvested leaves using a photoelectric leucometer (Dr Bruno Lange, Berlin).

For *Protea nitida*, which had a very sparse crown, leaf

area index was measured by harvesting and measuring all leaves after mapping the canopy area. For the other species, a vertical cylinder with a cross-sectional area of 0.26 m^2 was drawn at 5 or 6 random positions through the canopy, and all leaves clipped from within each cylinder. Leaf areas were determined thus for each sample unit, and a mean leaf area index for each species was calculated.

One-year-old leaves of each species were collected in February 1986 for the determination of total nitrogen content in foliar digest (Nicolson 1984).

Plant water relations and net leaf photosynthesis

Leaf xylem pressure potentials were measured during August, October, November and December 1986 and January and February 1987. Two typical plants were chosen for each species. Xylem pressure potentials were measured for shoots about 100 mm long or for leaves, depending on the size of the leaf. Hourly measurements were made starting at 05:00 and usually continuing until 19:00.

Plant water relations and photosynthesis were measured during August 1986 (late winter) and in January and February 1987 (mid- to late summer). Measurements were also made during October 1987 for the hillslope species. Measurements were made on warm days with cloudless or nearly cloudless skies. Hillslope and riparian plants could not be measured on the same day and measurements were usually made two days apart. In most cases, weather conditions were very similar on these days.

Simultaneous measurements were made of net leaf photosynthesis (P_n), transpiration (E_l) rates and leaf conductance (including stomata, cuticle and boundary layer conductances) (g_s) using a portable infra-red gas analyzer (Analytical Development Company Model LCA-2) in the open system and differential mode. Hourly measurements were made on 4–6 leaves starting as soon as leaves were dry (usually about 08:00) and usually continuing until 18:00. Measurements were made on leaves fully exposed to the sun at a height of 1 to 2 m above the ground on the eastern side of the plant. Single leaves were placed into the cuvette into which a measured flow of air of known water vapour and carbon dioxide concentration was pumped. Net photosynthesis and transpiration rates were determined from the flow rate and the concentration differences of CO_2 and H_2O between inlet and exhaust air according to Jarvis (1971) and Jarvis & Sandford (1985). Photosynthetically active radiation (*PAR*) incident on the leaf, air temperature within the cuvette, ambient relative humidity and temperature (for calculation of *VPD*) were measured with each reading. Leaf temperature (T_l) was calculated from the energy budget of the leaf using the equation:

$$T_l = T_a + dt \qquad (1)$$

where $dt = (H - LHV \times E_l)/[0.93 \times MA \times CP/r_b + (4.5 + T_a/16.0)]$,
H is the radiation absorbed by the leaf (J m^{-2} s^{-1}) and is assumed to be 17.5 % of *PAR*, *LHV* is the latent heat of vapourization of water, E_l is the transpiration rate, *MA* is the molecular weight of air, *CP* is the specific heat at constant temperature, r_b is the boundary layer resistance to water vapour, and T_a is the air temperature (Analytical Development Company 1985). Stomatal resistance (r_s) was calculated as:

$$r_s = (e_s/e_0 - 1)\, W - r_a \qquad (2)$$

where e_s is the saturated vapour pressure at leaf temperature, e_0 is the water vapour pressure in the air emerging from the cuvette, W is the mass flow of air per unit leaf area and r_a is the boundary layer resistance over the leaf. Leaf conductance (g_s) is the reciprocal of r_s.

Regular measurements of leaf conductances were also made on two leaves of each tree or shrub on each day of measurement using a null-balance diffusive resistance porometer of the Beardsell type (Beardsell *et al.* 1972). Leaves selected for this purpose were from the current crop, fully expanded, and represented the modal leaves of fully exposed shoots. Measurements were made on the same two leaves on each tree or shrub throughout the day. These measurements were used for the determination of daily mean maximum leaf conductances for each species (the median value computed from all measurements made between 09:00 and 11:00). The median, rather than the mean, was used to reduce the significance of outliers, particularly very low values.

Leaf conductances, transpiration and net photosynthesis rates are presented on a projected leaf area basis.

Water-use efficiency (*WUE*) was calculated as an instantaneous ratio of P_n to E_l (μmol CO_2/mmol H_2O).

Approximate light response curves for the five species were derived by pooling all data and plotting *PAR* against P_n and fitting a curve to maximum values of P_n. This should indicate the response of P_n to *PAR* when no other factors are limiting (Jarvis 1976).

Results

Climatic conditions

August (360 mm) and September (121 mm) were the wettest months during the study period (67% of rain for the period 1 August 1986 to 28 February 1987 fell during these months). December (31 mm) and February (26 mm) were the driest. Only 5 mm of rain fell between 2 and 31 December 1986. Despite this, the summer of 1986/7 was wetter than average; 165 mm of rain fell between 1 December 1986 and 28 February 1987 (149% of the 50-year-average). Of the days on which measurements were made of plant water relations, 13 January (7; hillslope species) and 15 January 1987 (9; riparian species) were the driest (numbers in parentheses are the number of days since last rain). This period also shows the lowest daily minimum relative humidities and highest daily maximum temperatures and water vapour pressure deficits (Figure 1). Air temperature exceeded 35°C and *VPD* exceeded 4.5 kPa only twice during the study period (Figure 1).

Despite the mediterranean rainfall regime in the average year at Jonkershoek, there was no pronounced drought during the study period (we define a 'drought' as a period during which daily rainfall never exceeded 0.5 mm). Droughts of 30 days or longer have occurred

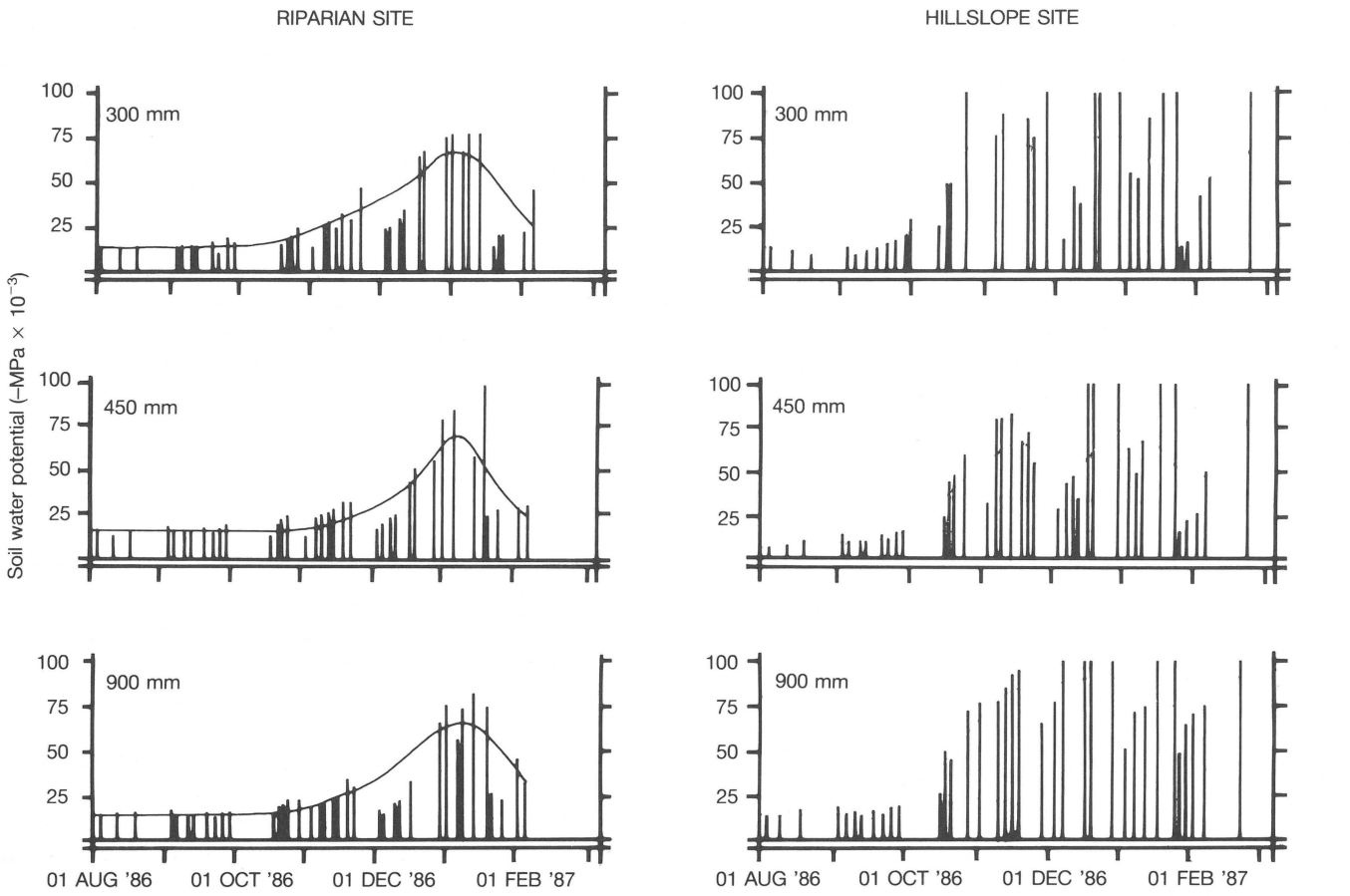

Figure 2 Seasonal progression of soil moisture potential at depths of 300 mm, 450 mm and 900 mm at the hillslope and riparian sites. Measurements were made with porous cup tensiometers with a maximum of 0.1 MPa. The maximum was exceeded on several days at the hillslope site. The smoothed lines, fitted by spline interpolation (SAS Institute Inc. 1985), indicate average time trends at the riparian site.

only 12 times at Swartboskloof since 1936 (i.e. only once every 4.2 years on average). Droughts of 40 days or longer occurred once every 8.3 years on average. The longest period without a daily rainfall exceeding 0.5 mm during this study was 17 days.

Soil water potential

At the riparian site, soil water potentials at 300 mm remained above –0.05 MPa until mid-December, and did not reach –0.1 MPa during the study period (Figure 2). Potentials at 900 mm of –0.05 MPa or lower were recorded only during January 1987. At the hillslope site, however, potentials at 300 mm frequently dropped below the –0.1 MPa capacity of the tensiometers, even during October 1986. At this site, soil water potentials at 900 mm were regularly below –0.05 MPa after mid-October, and were below –0.1 MPa for much of December and January. Even during summer, soil moisture at 900 mm was recharged rapidly and regularly following relatively light rainfall events (Figure 2).

These results show the spatial gradient in soil water potential between the hillslope and riparian sites, and the temporal gradient at both sites between the wet winter and the dry summer.

Plant form and characteristics of foliage and canopy

Although the patterns were not completely consistent, the hillslope and riparian species tended to differ significantly, in foliage (Table 1) and canopy characteristics (Table 2). All species were sclerophyllous but specific leaf area (surface area/fresh mass) was lowest for the two *Protea* species. Leaves of the hillslope shrubs were more vertically inclined and had lower absorptances than those of the riparian habitat. Both features suggest selection for stress avoidance (Ehleringer & Comstock 1987). Absorptances (63 to 70%) are slightly below the range reported for sclerophyllous plants in California and Chile (70 to 87%; Ehleringer & Comstock 1987), but this may be due to differences in methodology. *Brachylaena neriifolia* and *Cunonia capensis* had higher leaf area indices than the other species, about double on average. The two *Protea* species have amphistomatous leaves whereas the riparian trees all exhibit hypostomaty. Stomatal densities (average for both surfaces) were higher in the riparian species.

Photosynthetic characteristics of leaves

There were no consistent differences between hillslope and riparian species in light response (Figure 3).

Table 1 Leaf characteristics of riparian trees and hillslope shrubs selected for study at Swartboskloof (R = riparian; H = hillslope). Sample sizes: leaf area and width (n = 30); specific mass (n = 10); stomatal density (n = 5 or 6); azimuths and angles (n = 20); absorptance (n = 1) and leaf nitrogen (n = 3). Standard errors are given in parentheses

Species	Area (mm^2)	Width (mm)	Specific leaf area ($mm^2\ g^{-1}$)	Stomatal density (mm^{-2}) Adaxial	Stomatal density (mm^{-2}) Abaxial	True azimuth (°)	Median leaf angle (°)	Absorptance Adaxial	Absorptance Abaxial	Leaf nitrogen content (%)
Brabejum stellatifolium (R)	1901(139)	24.4(1.0)	2607.2(46.4)	0	296.9(10.4)	354.6	57.5	0.70	0.69	1.00
Brachylaena neriifolia (R)	1050(48)	13.4(0.4)	2880.8(137.7)	0	290.2(18.4)	168.0	59.0	0.70	0.63	0.95
Cunonia capensis (R)	1558(52)	22.5(0.5)	2764.1(64.5)	0	250.0(13.3)	357.8	60.0	0.72	0.69	1.06
Protea nitida (H)	3581(137)	36.7(0.8)	1413.2(21.9)	109.4(5.2)	121.5(9.7)	278.9	12.5	0.63	0.63	0.85
Protea repens (H)	693(23)	8.6(0.2)	2565.1(95.0)	52.1(0)	52.1(0)	157.5	22.5	0.70	0.68	0.63

Cunonia capensis, however, had a markedly lower maximum net photosynthesis rate than the other species.

Diurnal cycles

Maximum air and leaf temperatures were reached between 12:30 and 15:30 on all days at both sites (Figures 4–8). The *VPD* increased to a maximum between 13:30 and 16:00 on all days. The difference between early morning and maximum *VPD* was greatest on 22 October 1986 and during January 1987. There were no marked differences in daily courses of air temperature and *VPD* at the two sites.

Maximum PAR incident on the leaves occurred between 11:00 and 14:00, and is close to the potential maximum arriving at the earth's surface (Nobel 1977).

In general, leaf xylem pressure potential decreased with increasing environmental water stress brought on by the increasing irradiance, temperature and *VPD*. Potentials decreased to daily minima between 11:00 and 16:00 for all species at both sites. Even during January 1987, leaf xylem pressure potentials for the hillslope species returned to above –1.0 MPa after 16:00. This suggests that the midday depressions in leaf xylem pressure potentials were caused by water loss through transpiration, and not by water restrictions in the vicinity of roots, even for the shrubs at the hillslope site.

Maximum daily leaf conductances for all species were realized between 09:00 and 11:00. For the hillslope species, conductances remained fairly constant during the day on 18 August. On 22 October, conductance for *Protea repens* declined constantly through the day and showed no recovery in the afternoon (Figure 8). *Protea nitida*, however, shows a more constant daily course, with an increase in the late afternoon (Figure 7). On this day, *P. repens* showed a much lower midday leaf xylem pressure potential (–2.1 MPa) than *P. nitida* (–1.4 MPa), and this probably explains the observed difference in stomatal behaviour. During January and February 1987, leaf conductances were depressed around midday in both hillslope species. Maximum morning rates were reached between 09:00 and 11:00, after which rates declined to minima between 13:00 and 14:30 and then increased after 14:00–15:00 to regain (or nearly) early morning rates at 15:00–17:30 (Figures 7 & 8). All species at the riparian site showed fairly constant conductances throughout the day on 20 August 1986, although *Brabejum stellatifolium* and *Brachylaena neriifolia* showed poorly defined peaks at 09:00–11:30 and 14:00–16:30 (Figures 4 & 5). On 15 January 1987,

Table 2 Tree/shrub height, rooting depth and leaf area index for selected species of riparian and hillslope habitats at Swartboskloof, south-western Cape (R = riparian, H = hillslope)

Species	Height (m)	Rooting depth (m)	Leaf area index
Brabejum stellatifolium (R)	4.0	To water table	1.96
Brachylaena neriifolia (R)	4.0	To water table	5.30
Cunonia capensis (R)	7.5	To water table	6.26
Protea nitida (H)	3.0	3 m+	2.36
Protea repens (H)	4.0	3 m+	2.10

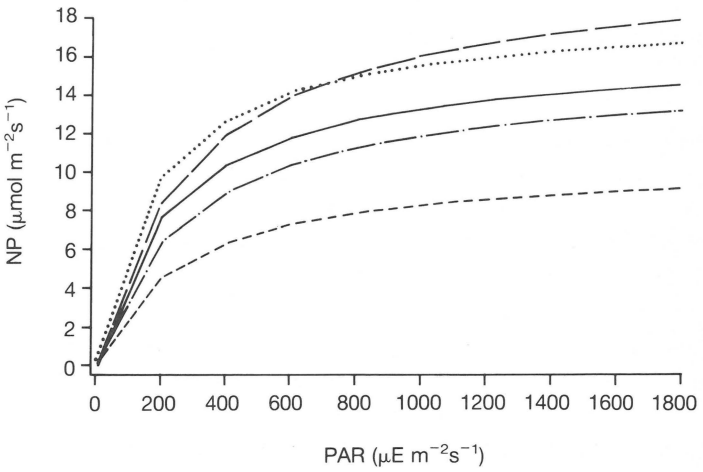

Figure 3 Light response curves for *Brabejum stellatifolium* (——), *Brachylaeana neriifolia* (....), *Cunonia capensis* (– – –), *Protea nitida* (·—·—·) and *Protea repens* (— —) at Swartboskloof. Approximate response curves were derived by plotting pooled data from field measurements over 7 months and fitting a rectangular hyperbole to maximum values of P_n (Jarvis 1976; Long & Hallgren 1985).

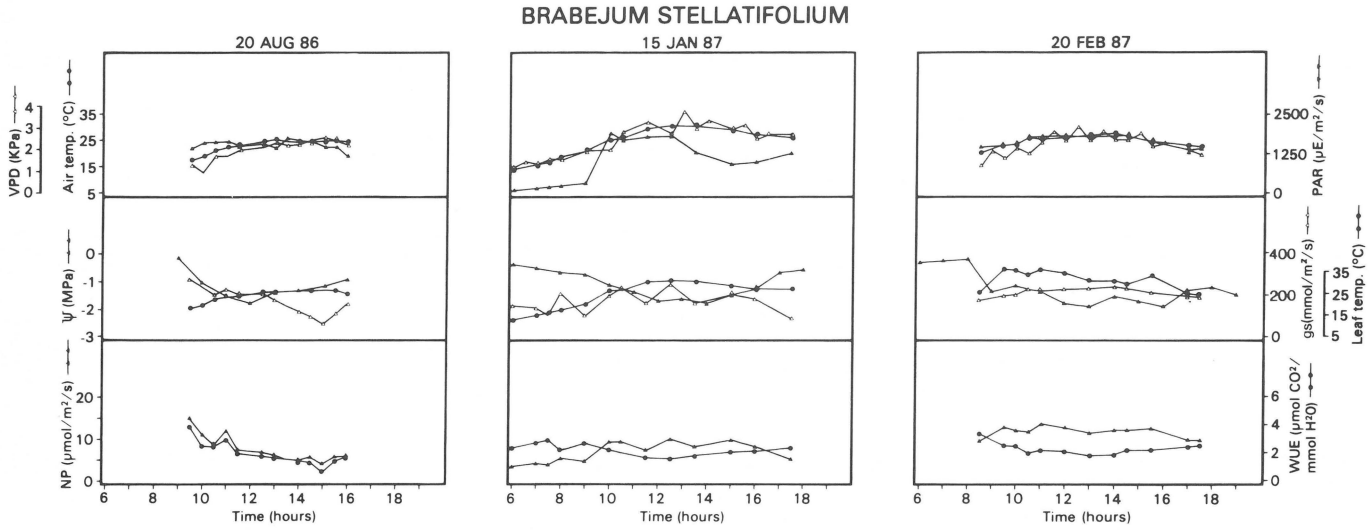

Figure 4 Daily courses of vapour pressure deficit (*VPD*), air temperature, photosynthetically active radiation (*PAR*) incident on the leaf, leaf xylem pressure potential (ψ), leaf conductance (g_s), leaf temperature, net leaf photosynthesis (*NP*) and water use efficiency (*WUE*) for *Brabejum stellatifolium*.

when midday *VPD*'s exceeded 3.5 kPa, *Brabejum stellatifolium* maintained fairly constant conductance rates throughout the day, whereas *Brachylaena neriifolia* and *Cunonia capensis* showed two-peaked courses. Midday leaf xylem pressure potentials for the last-mentioned two species were higher (less negative) than for *B. stellatifolium*. The differences in orientation and dimensions of leaves evidently influence the respective heat balances of the species of the two habitats. Measurements on 6 February 1987 with the leaf thermocouple of a Li-Cor Li1600 porometer showed that the leaf temperatures of the *Protea* species closely followed ambient air temperatures, the maximum leaf temperatures being 2–3°C above ambient. By contrast, the leaves of *Cunonia capensis* exceeded ambient temperatures by up to 6–7°C around midday when the ambient temperatures reached 26°C. Leaf conductances of the hillslope species declined on all days when the maximum *VPD* exceeded 3.0 kPa (Figures 7 & 8). Vapour pressure deficits of this magnitude did not cause similarly marked stomatal closure in the riparian species (Figures 4, 5 & 6).

Diurnal cycles of net leaf photosynthesis for all species followed closely the diurnal cycles of leaf conductance (Figures 4–8). Patterns of water-use efficiency were remarkably similar for hillslope and riparian shrubs. Diurnal changes in WUE were more marked in the hillslope species, especially during the summer (Figures 7 & 8), when photosynthesis rates were highest in the early morning and lowest at midday. *WUE* was slightly higher for hillslope shrubs during August 1986, when maximum *WUE* approached 4 µmol CO_2/mmol H_2O at around 09:00.

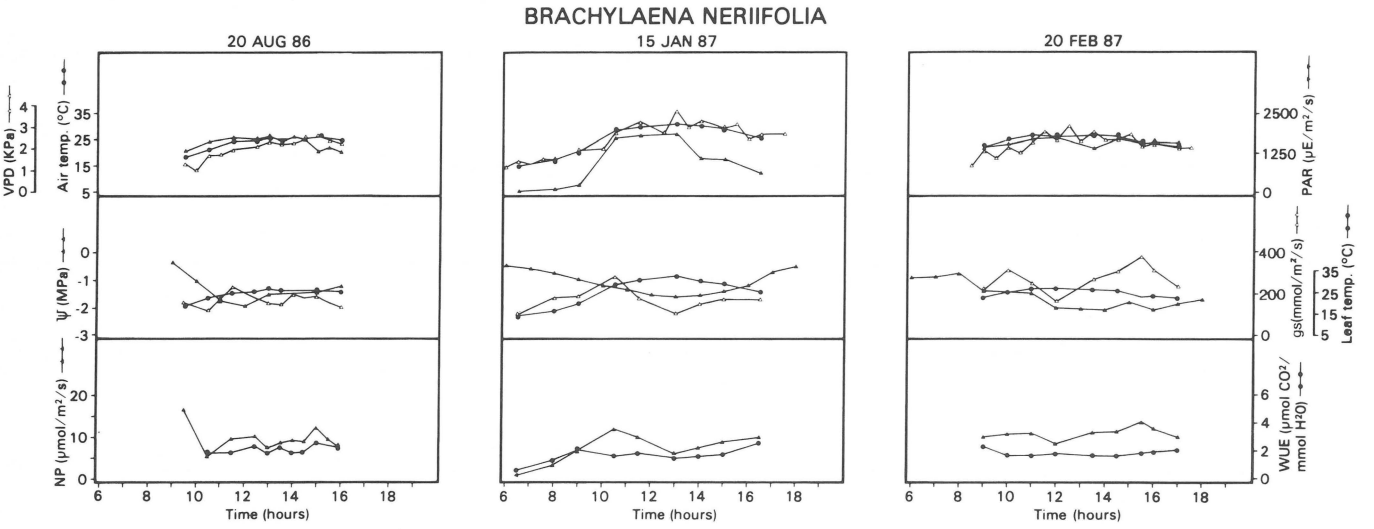

Figure 5 Daily courses of vapour pressure deficit (*VPD*), air temperature, photosynthetically active radiation (*PAR*) incident on the leaf, leaf xylem pressure potential (ψ), leaf conductance (g_s), leaf temperature, net leaf photosynthesis (*NP*) and water use efficiency (*WUE*) for *Brachylaeana neriifolia*.

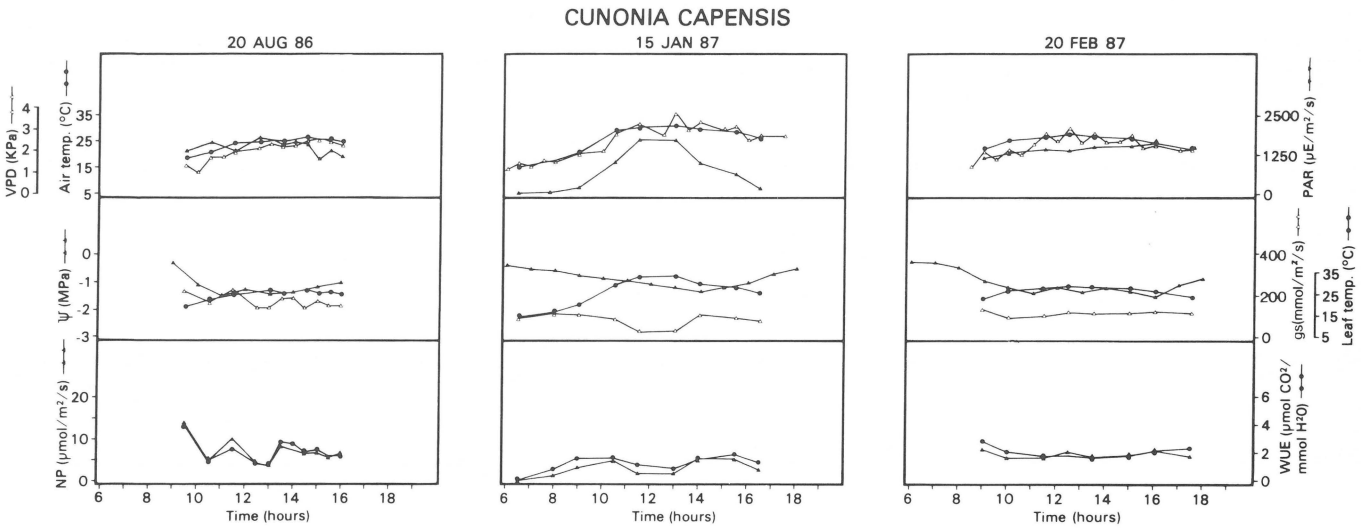

Figure 6 Daily courses of vapour pressure deficit (*VPD*), air temperature, photosynthetically active radiation (*PAR*) incident on the leaf, leaf xylem pressure potential (ψ), leaf conductance (g_s), leaf temperature, net leaf photosynthesis (*NP*) and water use efficiency for *Cunonia capensis*.

Seasonal differences

Leaf xylem pressure potentials

Predawn leaf xylem pressure potentials remained fairly constant for all species between August 1986 and January 1987 (Figure 9). *Protea repens* showed the lowest (most negative) potentials throughout this period. During February 1987, both hillslope species and *Brachylaena neriifolia* showed pre-dawn potentials below –0.5 MPa, while *Brabejum stellatifolium* and *Cunonia capensis* maintained pre-dawn potentials of about –0.2 MPa. The minimum pre-dawn potentials recorded during this study are much higher (less negative) than those for shrubs of similar structure in chaparral. For example, during extreme drought in mediterranean-climate California, pre-dawn potentials of *Adenostoma fasiculatum* and *Arctostaphylos stanfordiana* drop below –3.0 MPa (Hart & Radosevich 1987).

Midday leaf xylem pressure potentials remained above –2.0 MPa for all species except *Protea repens* between August 1986 and the end of January 1987. On 15 December 1986, the minimum potential for *P. repens* was –2.15 MPa. During February 1987, all species except *Cunonia capensis* showed midday potentials below –2.0 MPa. The two hillslope species, *Protea nitida* and *P. repens* showed minimum potentials of –2.75 MPa and –2.65 MPa respectively. These minima are lower than the minimum midday potentials recorded by Miller *et al.* (1983a) and Miller *et al.* (1984) for *Protea neriifolia, P. nitida* and *P. repens* at Swartboskloof, and for *P. laurifolia* at Algeria in the Cederberg during the summer of 1981/2. The lowest leaf xylem pressure potentials for *P. nitida* and *P. repens* recorded during our study are much higher (less negative) than the lowest potentials reported for sclerophyllous trees and shrubs in other mediterranean-climate regions. For example, Davis & Mooney (1986) and Hart & Radosevich (1987) recorded minimum potentials below –6.0 MPa for *Rhamnus californica* and *Arctostaphylos stanfordiana* during the summer in mediterranean-climate California

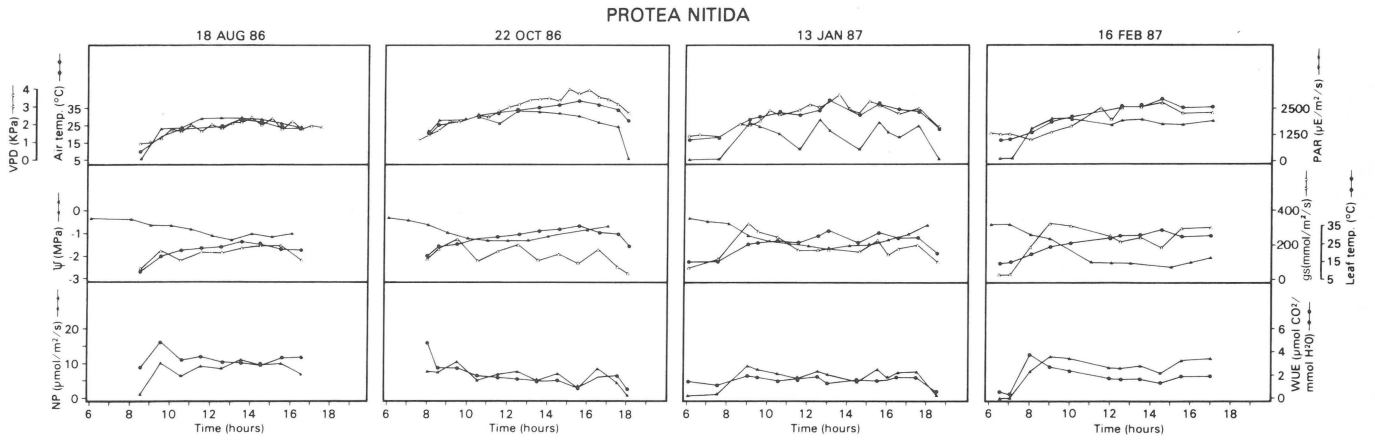

Figure 7 Daily courses of vapour pressure deficit (*VPD*), air temperature, photosynthetically active radiation (*PAR*) incident on the leaf, leaf xylem pressure potential (ψ), leaf conductance (g_s), leaf temperature, net leaf photosynthesis (*NP*) and water use efficiency for *Protea nitida*.

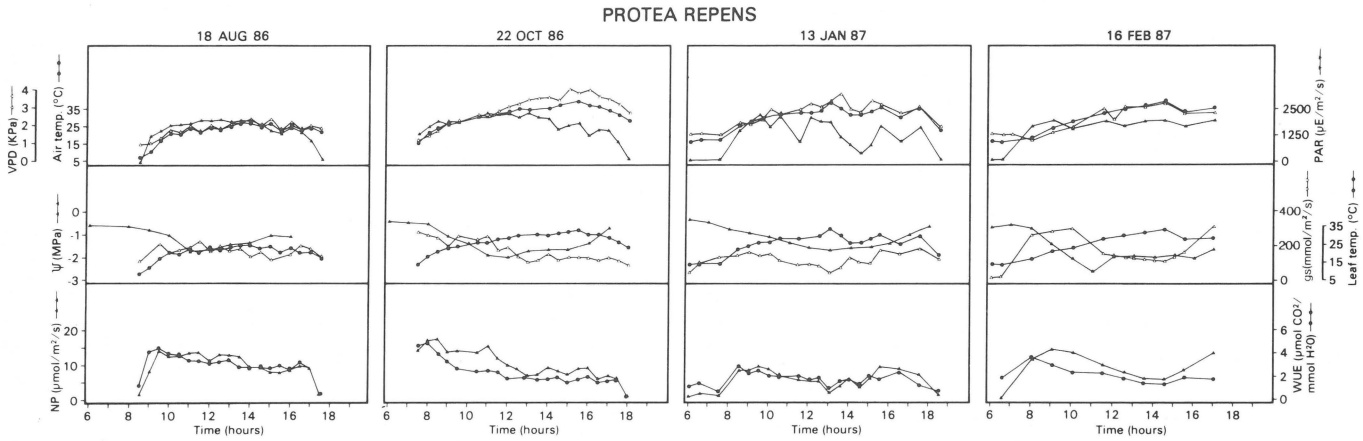

Figure 8 Daily courses of vapour pressure deficit (*VPD*), air temperature, photosynthetically active radiation (*PAR*) incident on the leaf, leaf xylem pressure potential (ψ), leaf conductance (g_s), leaf temperature, net leaf photosynthesis (*NP*) and water use efficiency for *Protea repens*.

respectively.

Daily ranges in leaf xylem pressure potential varied from 0.85 to 2.00 MPa for the riparian trees and from 1.10 to 2.15 MPa for the hillslope shrubs. It is not only the absolute minimum leaf xylem pressure potential reached during the day, but also the time that the potential remains low that determines the effect on stomatal behaviour (see Nilsen *et al.* 1983: 1386). For *P. nitida*, leaf xylem pressure potential declined below –2.0 MPa only on 16 February 1987 and remained below this value for 6 h. Potentials remained below –1.5 MPa for 5 h and 8 h on 13 January and 16 February respectively. *Protea repens* was subject to low potentials for longer than *P. nitida*; 2, 5, 4 and 8 h below –1.5 MPa on the 4 days, but only for 1 h and 2 h below –2.0 MPa on 22 October and 16 February. Among the riparian trees, only *Brachylaena neriifolia* experienced leaf xylem pressure potential below –2.0 MPa during the study; for 4 h on 20 February. *Brabejum stellatifolium* and *Brachylaena neriifolia* experienced similar water stress, as shown by the number of hours with leaf xylem pressure potentials of –1.5 MPa or lower. *Cunonia capensis* experienced leaf xylem pressure potentials below –1.5 MPa for only 1 h on 20 August and 1 h on 20 February.

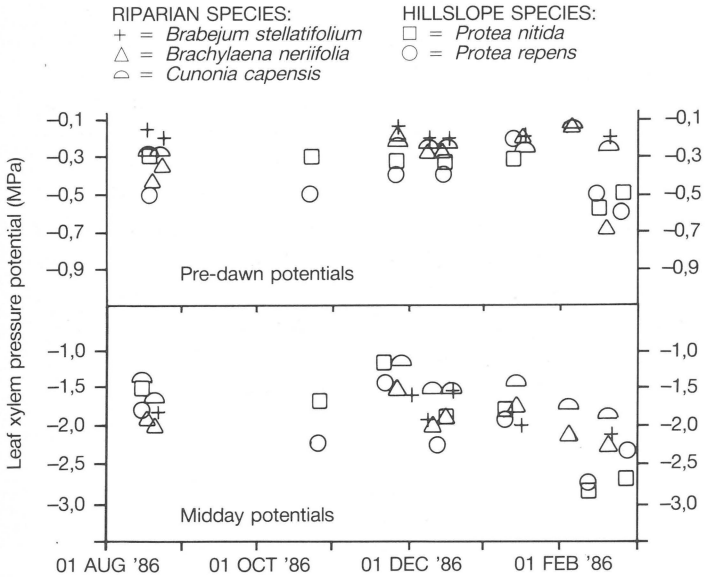

Figure 9 Seasonal progression of pre-dawn and midday leaf xylem pressure potentials of trees and shrubs at the hillslope and riparian sites.

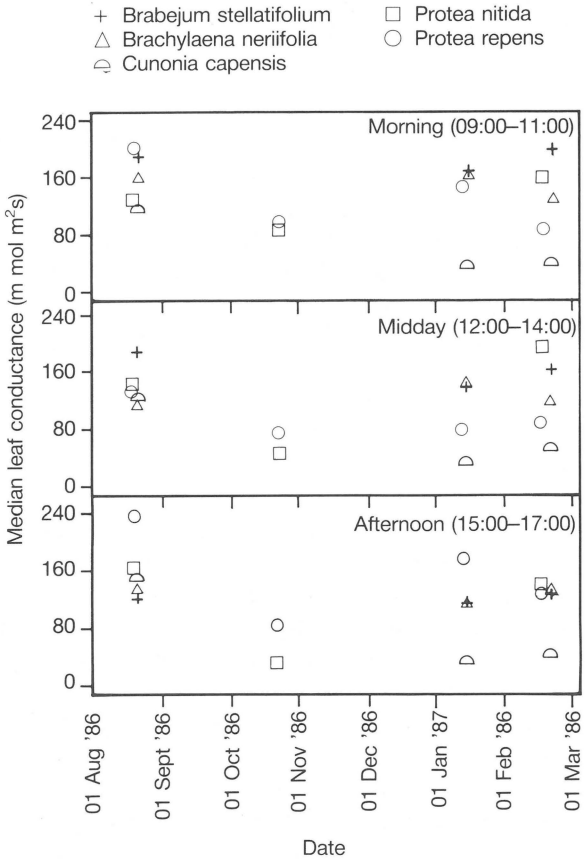

Figure 10 Seasonal progression of leaf conductance in the morning (09:00-11:00), midday (12:00-14:00) and afternoon (15:00-17:00). For each period, the median of 4–8 readings was taken.

Seasonal progression of daily maximum conductance and net leaf photosynthesis

For all species at both sites, the highest daily maximum leaf conductance rates were recorded during August. *Protea repens* had the highest daily maximum rate during August (200 mmole m^{-2} s^{-1}; calculated as the median of readings taken between 09:00 and 11:00). The other species showed daily maximum rates of between 120 and 200 mmole m^{-2} s^{-1} and there was no clear difference between hillslope and riparian species in this respect (Figure 10). Daily maximum leaf conductance during January and February was lowest in *Cunonia capensis*, and highest in *Brabejum stellatifolium*. Again, there was no consistent difference between hillslope and riparian species in this respect (see also Kruger *et al.* 1988; Richardson & Kruger 1988). There was no significant difference between early morning and midday or afternoon conductance rates for any of the species, even during summer (Figure 10). Maximum leaf conductances were similar to those reported for *P. neriifolia* at Swartboskloof (Miller *et al.* 1983a) and for a range of sclerophyllous trees and shrubs in the chaparral and matorral (Poole *et al.* 1981).

There were no clear seasonal trends in maximum daily net leaf photosynthesis. For all species at both sites, the daily maximum rates during August 1986 were approximately the same as those recorded during February 1987. All species, however, showed reduced maximum rates of CO_2 uptake during January 1987 (Figures 4–8), when the summer drought was most pronounced (Figures 1 & 2).

Discussion

Despite the differences in habitat [shown by the contrasting conditions of soil water potential (Figure 2)] and leaf and canopy characteristics between the hillslope and riparian species (Tables 1 & 2), there is little in our results to indicate real differences in their stomatal behaviour, net photosynthesis and water-use efficiencies.

The hillslope soils were significantly drier during summer than those on the banks of the perennial stream (Figure 2). These differences in soil moisture were reflected in the pre-dawn and midday xylem pressure potentials at the two sites (Figure 9), but the magnitude of the differences was much less than had been expected. Roots of the shrubs at the hillslope site penetrate to at least 3 m (Higgins *et al.* 1987) and probably deeper (pers. obs. at road cuttings). It appears that these shrubs behave as phreatophytes and tap water at depth. Soil water potentials at depths of 900 mm frequently dropped below –0.1 MPa but diurnal courses of conductance and net leaf photosynthesis during such 'droughts' do not suggest severe water stress. Rates return to early morning values after the midday depressions (see e.g. 13 January 1987 in Figures 7 & 8). The hillslope communities have sparser canopies than the riparian trees (Table 2) and evapotranspiration was apparently too low to dry the soils to this depth.

It appears that the canopy densities of sclerophyllous shrublands in mediterranean-climate regions equilibrate with actual evapotranspiration rates; higher actual evapotranspiration is associated with higher leaf area index (Miller *et al.* 1983b). This equilibrium causes summertime depletion of soil moisture (Specht 1972; Miller *et al.* 1983b). Although the soil moisture at the hillslope sites at Swartboskloof was depleted to some degree, the deficits were very mild compared with other mediterranean-climate habitats (*cf.* Miller & Poole 1979; Miller *et al.* 1983b; Davis & Mooney 1985). The sparse canopies of the hillslope vegetation at Swartboskloof have apparently not equilibrated with available soil moisture. This could be accidental, owing to inherently low capacities for resource capture and use (Stock & Lewis 1984). This, coupled with relatively short life spans of the shrubs (Kruger & Bigalke 1984), could mean that fynbos shrublands may never attain canopy equilibrium with water balance in high rainfall zones such as Swartboskloof. Although the canopy characteristics of hillslope shrubs and riparian trees at Swartboskloof were markedly different, the ecophysiological differences were not as great as was expected. There is some evidence of relatively subtle differences in stomatal response to water stress.

It is possible that water stress at the seedling stage could be more important than in established plants, and that this could prevent the invasion of forest species. Pre-dawn xylem pressure potentials of –2.0 and –3.0 MPa were measured for seedlings of *P. nitida* and *P. repens* at Swartboskloof during the dry summer of 1987/8. Resprouting adults of *P. nitida*, measured simultaneously, showed potentials of only –0.5 MPa [similar to those measured during this study (Figure 9)]. Experiments to test the effect of soil moisture deficits on seedlings of forest trees and hillslope shrubs are in progress at the Jonkershoek Forestry Research Centre (P.T. Manders pers. comm.).

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